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# Importance of philopatry and hydrodynamics in the recruitment of bioeroding sponges on Indonesian coral reefs

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**Abstract.** Increasingly frequent large-scale coral mortality events are occurring across the globe, leading to a rise in available reef substrata and promoting an increase in the abundance of other benthic taxa. One such group are bioeroding sponges, which can benefit considerably from reef degradation. However, the occupation of new substrates is partially reliant upon larval recruitment, and currently little is known about the factors affecting bioeroding sponge recruitment. In this study we investigated the potential drivers of bioeroding sponge recruitment using a 2-year deployment of experimental calcareous substrates across seven reefs in the Wakatobi region of Indonesia. Recruitment was observed for five bioeroding sponge species, namely *Cliona orientalis*, *Cliothosa* cf. *aurivillii*, *Cliothosa hancocki* and two presently unidentified brown clionaids, *Cliona* aff. *viridis* sp. A and *Cliona* aff. *viridis* sp. B. Recruits were present on 69% of the experimental substrates but had a low mean (±s.e.m.) spatial coverage of just 0.42 ± 0.13%. Total recruitment and species assemblage structure were correlated with local adult abundance, water flow and substrate cues. Our results suggest that any proliferation of bioeroding sponges on newly available substrate following coral mortality is likely to be conditional on local adult abundance and hydrodynamics.

**Additional keywords:** benthos, bioerosion, larvae.

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## Introduction

Coral reefs are in a state of global decline as sources of anthropogenic stress increase (Bellwood *et al.* 2004; Bruno and Selig 2007; De'ath *et al.* 2012; Jackson *et al.* 2014). In recent years, these declines have largely been attributed to man-made climate change and mass coral bleaching associated with thermal anomalies (Hughes *et al.* 2003, 2017; Eakin *et al.* 2010; DeCarlo *et al.* 2017). Historically, corals have dominated coral reef substrate through competitive interactions with less-competitive taxa. However, large-scale coral die-offs, associated with bleaching events (Glynn 1984; Normile 2016) and other stressors (Aronson and Precht 2001; Kayal *et al.* 2012), are increasingly exposing a greater proportion of bare calcareous substrate on coral reefs. On degraded and stressed reefs, where coral recruitment can be low (Kuffner *et al.* 2006; Hoey *et al.* 2011) and spatial competitive ability is reduced (Aerts 2000; Vermeij *et al.* 2010), other taxa can colonise and competitively maintain this substrate, preventing the re-establishment of hard coral dominance. For example, large-scale coral cover declines in the Caribbean have often coincided with regime shifts to macroalgal dominance (Lessios *et al.* 1984; Aronson and Precht 2001; Gardner *et al.* 2003; Mumby 2009; Eakin *et al.* 2010; Jackson *et al.* 2014). The situation appears to be different in the Indo-Pacific, where, despite some declines in coral cover (Bruno and Selig 2007), macroalgal-dominated reefs are rare (Bruno *et al.* 2009). This has led some authors (e.g. Norström *et al.* 2009; Bell *et al.* 2013) to question what other benthic taxa may occupy the space left by coral mortality and potentially dominate degraded reefs. Recent bleaching events (and subsequent coral mortality) have been associated with large increases in bioeroding sponge abundance on reefs across the globe (Sheppard *et al.* 2002; Schönberg and Ortiz 2009; Carballo *et al.* 2013). These increases and the resilience demonstrated by some bioeroding sponges to elevated water temperature and reduced pH have led several authors to propose bioeroding sponges as possible 'winners' on degraded coral reefs (e.g. Schönberg and Ortiz 2009; Chaves-Fonnegra *et al.* 2018).

The ability of bioeroding sponges to occupy newly available substrate following coral mortality is likely to occur through lateral encroachment, fragmentation, larval recruitment or a combination of these processes (López-Victoria and Zea 2004, 2005; Zilberberg *et al.* 2006; Chaves-Fonnegra and Zea 2011). Larval recruitment is vital for sponge population maintenance (Pineda *et al.* 2009, 2010; McMurray *et al.* 2010; Knapp *et al.*

2016), but may also be important for regulating adult distribution (Uriz *et al.* 1998) and supporting the expansion of a species into novel habitats. Recruitment rates in sponges are generally considered to be low (Zea 1993) and appear to be particularly low from the few studies that indirectly assessed recruitment in bioeroding sponges (Kiene and Hutchings 1994; Pari *et al.* 1998, 2002). Recruitment of internal bioeroders has been studied in French Polynesia and the Great Barrier Reef (GBR), and these studies have revealed a successional pattern from initial colonisation by polychaetes and sipunculans to an increasing abundance of boring molluscs and sponges with time (Kiene and Hutchings 1994; Pari *et al.* 1998, 2002; Tribollet *et al.* 2002).

Although sponges are capable of asexual reproduction and dispersal (e.g. López-Victoria and Zea 2004), the prevailing reproductive mode is sexual and dispersal relies on a free-living larval stage (Uriz *et al.* 2008). As such, recruitment is thought to be limited by larval production (Mariani *et al.* 2001; Piscitelli *et al.* 2011), survival (e.g. Uriz *et al.* 1996), dispersal (Maldonado 2006), habitat selection and settlement (Maldonado and Uriz 1998) and post-settlement survival (Maldonado and Young 1996; de Caralt *et al.* 2007). The presettlement lifespan of sponge larvae is generally short, with larvae normally only remaining in the water column for minutes to days and usually for less than 2 weeks (Maldonado 2006). Once larvae contact the seabed, substratum exploration occurs at a scale of centimetres to metres, and can last longer than the planktonic phase (Maldonado 2006). Little is known about the mechanisms that influence final settlement location selection, but chemical signals produced by conspecifics, competitors or substrates are thought to be involved, as is the case for other invertebrate larva (Pawlik 1992). Evidence for these cues in sponges (e.g. microbial biofilms) are only beginning to emerge (Whalan *et al.* 2008, 2012; Abdul Wahab *et al.* 2011; Whalan and Webster 2014).

Most of what is currently known about reproduction and recruitment in bioeroding sponges comes from studies on *Cliona celata*, *C. delitrix*, *C. tenuis* and *C. viridis*. From these studies, it appears that oviparous embryonic development is the most widespread in bioeroding sponges (although potentially with internal fertilisation; Rosell 1993; Mariani *et al.* 2000; Maldonado and Riesgo 2008; González-Rivero *et al.* 2013). Gamete development occurs on an annual cycle and release is usually a highly synchronised event that has been related to water temperature (Mariani *et al.* 2000; Piscitelli *et al.* 2011; González-Rivero *et al.* 2013). Clionidae larvae are clavabastula (Maldonado 2006; Maldonado and Riesgo 2008) and particularly weak swimmers, often exhibiting predominantly crawling rather than swimming behaviour (Mariani *et al.* 2000, 2001, 2006). Consequently, dispersal is low and philopatric (Mariani *et al.* 2006). There are exceptions to these generalisations; for example, the Caribbean sponge *C. delitrix* exhibits asynchronous and multiple spawning events, and has wide larval dispersal (<350 km; Chaves-Fonnegra *et al.* 2015, 2016)

Despite some studies indirectly investigating bioeroding sponge recruitment within the Indo-Pacific (Kiene and Hutchings 1994; Tribollet *et al.* 2002), our knowledge of the drivers of recruitment is still very limited. Understanding these factors is important given the increase in potential habitat availability due to regional decreases in coral cover (Bruno and Selig 2007). Declines in coral cover may not only promote habitat availability for bioeroding sponges, but also the abundance of other benthic taxa that may act as cues for sponge recruitment. This study focused on the recruitment of bioeroding sponges on Indonesian coral reefs. Using a 2-year deployment of experimental calcareous substrates, recruitment was analysed in relation to water flow, substrate composition and local adult sponge abundance.

## Materials and methods

### Study area

This study was conducted within the Wakatobi UNESCO Biosphere Reserve in south-east Sulawesi, Indonesia. Bioeroding sponge recruitment was studied at seven reef sites fringing the islands of Hoga and Kaledupa (Fig. 1; Table 1; Marlow *et al.* 2018*a*). The sites (Buoy 1, Buoy 3, Kaledupa 1, Kaledupa Double Spur, Pak Kasim's, Ridge 1 and Sampela 1; abbreviated as B1, B3, K1, KDS, PK, R1 and S1) were chosen to represent a variety of reef types, environmental conditions and levels of reef degradation.

This research was conducted under a permit (182/SIP/FRP/E5/Dit.KI/VI/2016) from the Indonesian Ministry of Research and Technology (RISTEK).

### Bioeroding sponge recruitment

Bioeroding sponge recruitment was studied using a 2-year deployment of experimental calcareous substrates. The cubic calcareous recruitment blocks (10 × 10 × 10 cm) were made of cemented reef rock (limestone) obtained from a mine on the local coralline island of Wanci. The blocks were sourced in this way because the local availability of suitable dead coral was insufficient. Furthermore, previous work (Marlow *et al.* 2018*b*) has established the ecological relevance of these blocks, because bioeroding sponges erode into them at the same rates as into *Porites lutea*, a locally abundant coral species. Prior to deployment, recruitment blocks were cleaned with a wire brush (but not chemically cleaned) and cured in seawater for 24 h. Deployment occurred in July and August 2014; at each of the seven sites and at depths of 10 and 5 m, five blocks were attached 15 m apart to suitable patches of dead substrate using marine epoxy ($n = 70$). Each block was then photographed in reference to notable reef features to aid future recovery.

In July and August 2016, the recruitment blocks were recovered from the reef sites. Upon locating each block, each exposed side of the block was examined for any bioeroding sponges, noting species presence and location and the presence of any taxa that may be mistaken for sponges during image analysis. Blocks were then photographed *in situ* (every exposed side) and removed from the reef. In the laboratory, each block was subsequently split open using a hammer and chisel to either confirm in-water observations or locate previously unobserved sponges.

Recruitment was analysed using the *in situ* images and imaging software VidAna (ver. 1.0.1, J. Hedley, The University of Queensland, St Lucia, Qld, Australia, see http://www.marinespatialecologylab.org/resources/vidana/). From the images of each side of the block, recruits were located (with the aid of field notes) and marked (Fig. 2). Recruitment was

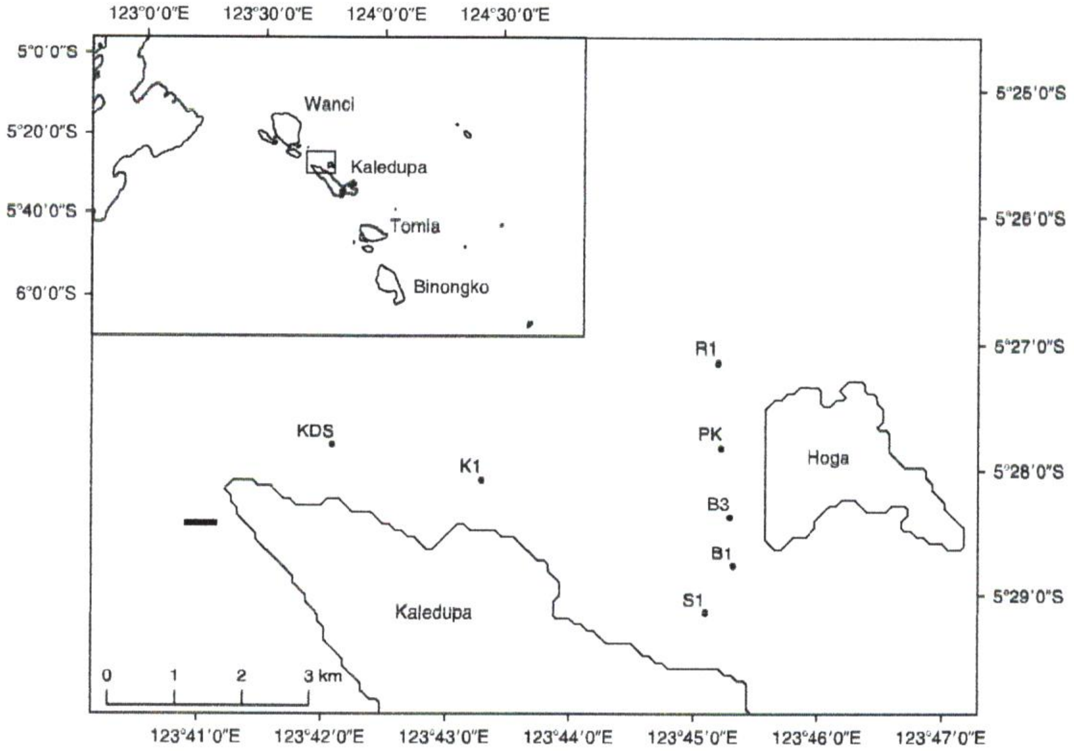

**Fig. 1.** Map of sponge recruitment study sites within the Wakatobi UNESCO Biosphere Reserve in south-east Sulawesi. B1, Buoy 1; B3, Buoy 3; K1, Kaledupa 1; KDS, Kaledupa Double Spur; PK, Pak Kasim's; R1, Ridge 1; S1, Sampela 1.

**Table 1. Reef site descriptions**

Coral cover data sourced from Marlow *et al.* (2018*a*), stressor information sourced from Clifton *et al.* (2010)

| Reef | Reef type | Live coral (%) | Main localised stressors |
|---|---|---|---|
| Buoy 1 | Steep wall | 19 | Fisheries |
| Buoy 3 | Steep wall | 34 | None |
| Kaledupa 1 | Sloping reef | 11 | Fisheries |
| Kaledupa Double Spur | Sloping reef | 15 | Fisheries |
| Pak Kasim's | Sloping reef | 24 | None |
| Ridge 1 | Steep wall | 28 | Fisheries |
| Sampela 1 | Sloping reef | 12 | Fisheries, sedimentation, coral mining |

measured in terms of percentage cover of sponge recruits (per species) in relation to the total area of the recruitment block side. Each side of the recruitment block was considered a subsample and data was averaged over all five sides of the block.

Previous research (J. Marlow, J. J. Bell, A. Haris, M. Shaffer, and C. H. L. Schönberg, unpubl. data) has used macromorphological differences and spicule and phylogenetic analyses to identify the common bioeroding sponge species of the Wakatobi region. That research identified eight bioeroding sponge species, namely *Cliona orientalis*, *Cliona* cf. *schmidtii*, *Cliothosa* cf. *aurivillii*, *Cliothosa hancocki*, *Spheciospongia* cf. *vagabunda*, *Zyzzya criceta* and two unknown clionaids, *Cliona* aff. *viridis* sp. A and B. These species are recognisably differentiable at the macromorphological level and so, in the present study, bioeroding sponges species were identified by the naked eye. In the rare occurrences of identification uncertainty, species identity was confirmed by spicule analysis of bleach-dissolved tissue using light microscopy.

### Biotic and abiotic predictor variables

Data were collected to determine the extent to which bioeroding sponge recruitment was correlated with the local adult population, substrate cues or flow.

The local adult bioeroding sponge population and substrate composition adjacent to each recruitment block were assessed using photographic quadrats, with images taken during block deployment in 2014. Each 1-m$^2$ quadrat was divided into 16 subdivisions and centrally placed around every recruitment

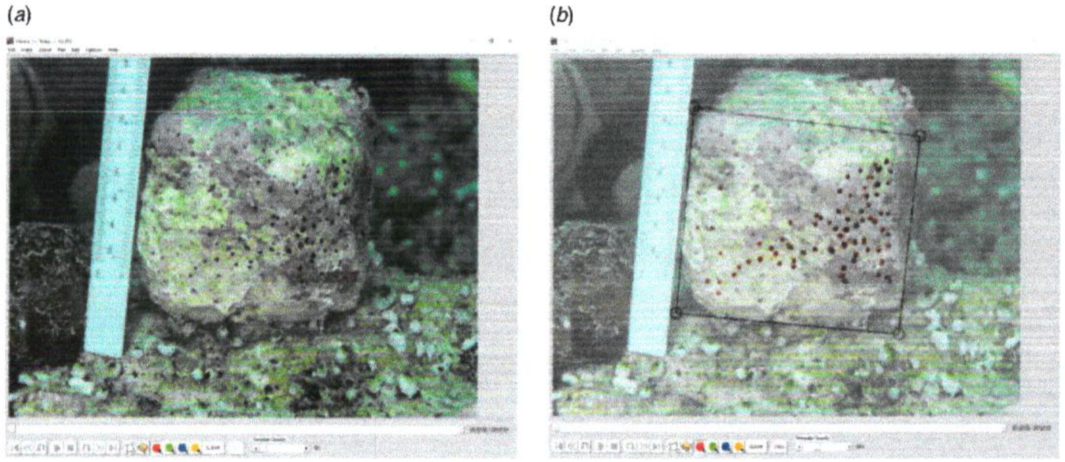

**Fig. 2.** Example screen shots of the VidAna software (ver. 1.0.1, J. Hedley, see http://www.marinespatialecologylab.org/resources/vidana/). (*a*) Image depicting one side of the recruitment block before measurement; (*b*) the same block after the recruits had been located and tagged.

block. Photographs were then taken of each subdivision, and the presence of any bioeroding sponges within the subdivisions was noted. The images of each photographic quadrat subdivision (and in combination with field notes) were subsequently examined using VidAna software; bioeroding sponge presence and cover was measured in terms of percentage cover of each species per subdivision. Benthic composition (other than bioeroding sponges) of the substrate adjacent to each block was measured using Coral Point Count (CPCe) software (https://cnso.nova.edu/cpce/index.html, accessed 1 December 2018; Kohler and Gill 2006). Fifteen points were randomly allocated to each subdivision image ($n = 240$ per photographic quadrat) and the substrate beneath each point was then allocated to one of the following categories: macroalgae, coralline algae (CCA), hard coral, sponge, soft coral, dead coral + algae, rubble, dead platform, recently dead coral (bleached), sand, silt, sediment on rock or 'other'. Bioeroding sponge cover and substrate composition data from each subdivision were averaged to create mean values for the entire square metre.

Analysis of the composition of the other benthic colonists of the recruitment blocks in 2016 was used to determine whether substrate cues at finer spatial scale were affecting bioeroding sponge recruitment. Previous studies have found that the recruitment of bioeroding sponges can take between 2 and 4 years (Kiene and Hutchings 1994; Pari *et al.* 1998, 2002; Tribollet *et al.* 2002). Therefore it was assumed that the majority of the other benthic types were already present on the blocks at the time of bioeroding sponge recruitment. The *in situ* images of recruitment blocks that were taken in 2016 for the purposes of sponge recruitment analysis were used for the analysis of the benthic composition of recruitment blocks. Twenty points were randomly allocated to each block side image ($n = 100$ per block) and the benthic taxa beneath each point identified as one of the following categories: ascidians, encrusting bryozoans, macroalgae, coralline algae, hard coral, soft coral, sponges, dead carbonate, settled sediment and 'other'. Data from each side of the block was taken as a subsample and averaged to create mean block benthic composition.

Flow rates were measured using mean proportional flow for each site by means of gypsum 'clods' (Doty 1971; Jokiel and Morrissey 1993). Clods were deployed for 24 h at depths of 10 and 5 m at each site on three occasions in June–August 2015, and proportional differences in water flow were determined from differences in percentage dry weight loss (see Marlow *et al.* 2018*b*).

### Statistical analysis

Univariate statistical analyses were performed in SPSS (ver. 23, IBM Corp., Armonk, NY, USA) to test the hypothesis that total recruitment differed among sites and between depths or was affected by the local abundance of adult bioeroding sponges, substrate cues or flow. To test the hypothesis that these same factors would also affect the assemblage composition of bioeroding sponge recruits, multivariate analyses were performed using the PRIMER-E (ver. 6, Plymouth Marine Laboratory, Plymouth, UK) with the permutational multivariate analysis of variance (PERMANOVA) add on.

### Bioeroding sponge recruitment analysis

Differences in total recruit abundance (all species combined) among sites and between depths was tested using a general linear model (GLM) and Tukey's *post hoc* tests using fourth root-transformed data. Correlations between recruit abundance and all biotic and abiotic predictor variables (localised substrate, block benthos, flow rates and adult bioeroding sponge abundance) were assessed using Spearman's rank correlation coefficient.

Sponge recruitment was highly variable; recruit assemblage data (average percentage cover per species per recruitment block) ranged from the very small (e.g. a single papillae) to quite large (e.g. many merging papillae) and contained many zeros. Therefore, the multivariate data was square root transformed and resemblance matrices were constructed using Bray–Curtis similarity coefficients. Because of the absence of bioeroding sponge recruits on many recruitment blocks, a dummy species with an abundance value of 1.0 was added to each recruitment block

**Table 2. Average percentage cover of bioeroding sponge recruits for individual species per site**

Data are given as the mean ± s.e.m. Also shown is total mean recruitment (all species combined) per site and mean for species across all recruitment blocks. Not shown are Species that did not recruit are not shown. B1, Buoy 1; B3, Buoy 3; K1, Kaledupa 1; KDS, Kaledupa Double Spur; PK, Pak Kasim's; R1, Ridge 1; S1, Sampela 1

| Site | *Cliothosa* cf. *aurivillii* | *Cliothosa hancocki* | *Cliona orientalis* | *Cliona* aff. *viridis* sp. A | *Cliona* aff. *viridis* sp. B | Total |
|---|---|---|---|---|---|---|
| B1 | 0 | 0 | 0 | 0 | 0.100 ± 0.060 | 0.100 ± 0.060 |
| B3 | 0.004 ± 0.003 | 0.008 ± 0.008 | 0 | 0 | 0.092 ± 0.030 | 0.104 ± 0.025 |
| K1 | 0 | 0 | 0 | 0.213 ± 0.140 | 0.058 ± 0.016 | 0.270 ± 0.194 |
| KDS | 0.036 ± 0.017 | 0 | 1.297 ± 0.500 | 0 | 0 | 1.333 ± 0.778 |
| PK | 0.218 ± 0.211 | 0 | 0 | 0.040 ± 0.040 | 0.026 ± 0.024 | 0.284 ± 0.220 |
| R1 | 0.040 ± 0.040 | 0 | 0.364 ± 0.342 | 0.012 ± 0.012 | 0.290 ± 0.240 | 0.706 ± 0.402 |
| S1 | 0.056 ± 0.030 | 0 | 0.007 ± 0.005 | 0 | 0.058 ± 0.013 | 0.120 ± 0.049 |
| Mean | 0.052 ± 0.033 | 0.001 ± 0.001 | 0.237 ± 0.125 | 0.034 ± 0.027 | 0.092 ± 0.038 | 0.417 ± 0.134 |

(Clarke *et al.* 2006). Differences in the composition of recruit assemblages among sites and between depths (and any interactions) were assessed using a two-factor PERMANOVA, and results were displayed graphically using principal coordinate analysis (PCO). The species of recruits that contributed most towards any site or depth differences were further investigated using similarity percentage analysis (SIMPER).

Differences in bioeroding sponge recruit assemblages were also analysed in relation to differences in biotic and abiotic explanatory variables using a distance-based multiple linear regression model (DistLM). Explanatory variables consisted of: (1) local adult bioeroding sponge abundance; and (2) benthic composition of the adjacent substrate and recruitment blocks (percentage cover), and flow rates. In order to find the most parsimonious model, Akaike's information criterion (AIC), a step-wise procedure, adjusted for small sample sizes (AICc) was used (Burnham and Anderson 2004). DistLM outputs were represented graphically with a distance-based redundancy ordination (dbRDA) in two-dimensional (2D) bubble plots of the highest recruiting species (species that recruited ≥10 recruitment blocks).

### *Benthic characterisation and flow analysis*

The significance of differences in the benthic composition of the recruitment blocks and adjacent substrate among sites and between depths was analysed using PERMANOVAs based on Bray–Curtis resemblance matrices constructed using square root-transformed data. These were characterised graphically using PCO with overlaying Pearson's correlation vectors. The same methodology was repeated to characterise the differences in assemblage composition of the adult bioeroding sponges adjacent to the recruitment blocks.

The significance of proportional differences in water flow rates (clod dissolution rates) among sites was tested using a GLM and Tukey's *post hoc* tests.

Where appropriate, data are given as the mean ± s.e.m.

## Results

### *Recruitment*

After 2 years of deployment, five species of bioeroding sponges had recruited to most of the deployed recruitment blocks, and bioeroding sponge recruits were present at every site and depth category.

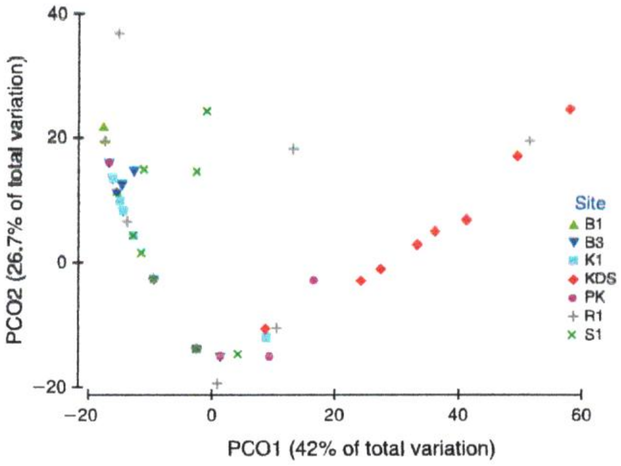

**Fig. 3.** Two-dimensional representation (principal coordinate analysis; PCO) of site similarities with regard to recruited bioeroding sponge species assemblage. B1, Buoy 1; B3, Buoy 3; K1, Kaledupa 1; KDS, Kaledupa Double Spur; PK, Pak Kasim's; R1, Ridge 1; S1, Sampela 1.

Of the 70 recruitment blocks deployed across the 7 reef sites, 65 were recovered and 45 of these (69.2%) had at least one sponge recruit. However, mean cover (0.42 ± 0.13%) and species richness (1.2 ± 0.1 species per block) were generally low. Average recruit cover ranged from 0.10 ± 0.06 at B1 to 1.3 ± 0.8% at KDS and was not significantly different among sites or between depths.

Five bioeroding sponge species were found to have recruited to the experimental substrate blocks. These species were *C.* aff. *viridis* sp. B (28 blocks), *Cl.* cf. *aurivillii* (11 blocks), *C. orientalis* (11 blocks), *C.* aff. *viridis* sp. A (3 blocks) and *Cl. hancocki* (1 block). Despite recruiting to the most number of blocks, *C.* aff. *viridis* sp. B was not as abundant overall as *C. orientalis*, predominantly due to large recruitment events for the latter species at KDS and R1 (see Table 2).

The assemblage composition of the recruits differed significantly among sites (PERMANOVA, pseudo $F = 3.876$, $P = 0.001$; Fig. 3), but not between depths; in addition, there was no interaction between sites and depths. SIMPER showed that the biggest differences occurred between KDS and both K1 and B1 (both 100% dissimilarity), driven by the dominance of *C. orientalis* in the KDS assemblage, which was absent at K1 and B1. The smallest differences were between B3 and S1 (63.98% dissimilarity), K1 and S1 (72.4% dissimilarity) and B3 and K1 (70.52% dissimilarity); at all these sites, *C.* aff. *viridis* sp. B was abundant, but the relative importance of other species, such as *C.* aff. *viridis* sp. A and *Cl.* cf. *aurivillii*, differed (Table 2).

### Biotic and abiotic variables

Local substrate composition adjacent to each block in 2014 differed significantly among sites (Fig. 4*a*) and between depths (Fig. 4*b*), and there was a significant interaction between depth and site (Table 3). The benthic community on the recruitment blocks in 2016 was also significantly different among sites, but not between depths and there was no significant interaction between site and depth (Table 3; Fig. 4*c*).

Significant differences in water flow (using the proxy clod dissolution) were found between the sites (GLM, $F_{(6,76)} = 16.906$, $P < 0.001$). *Post hoc* Tukey's tests showed that flow at KDS was significantly ($P < 0.05$) higher than all sites except K1, and that flow rates at B1 and B3 were significantly lower than at KDS, K1 and R1.

All eight regionally common species of bioeroding sponges (Marlow *et al.* 2018*a*) were found to be present in the 1 $m^2$ adjacent to the recruitment blocks. The species composition of these adjacent bioeroding sponge assemblages differed significantly among sites and between depths, but there was no significant interaction between site and depth (Table 3). Most sites were associated with assemblages that were dominated by *Cl.* cf. *aurivillii*, but KDS was characterised by a high abundance of *C. orientalis*, and several blocks at K1, KDS and R1 were adjacent to assemblages characterised by the presence of *C.* aff. *viridis* sp. A (Fig. 5)

### Effects of biotic and abiotic variables on recruitment

Total recruit percentage cover was positively correlated with local adult bioeroding sponge abundance ($r_s = 0.338$, $P = 0.006$; Fig. 6*a*) and flow ($r_s = 0.333$, $P = 0.007$; Fig. 6*b*), and was negatively correlated with the abundance of algae-covered dead coral in the adjacent substrate ($r_s = -0.318$, $P = 0.010$). None of the other measured biotic or abiotic variables was significantly correlated with total recruitment.

Variation in the local abundance of adult sponges explained 26.6% (Table 4) of the variation of the recruit assemblage composition, with the DistLM selecting three variables: *C. orientalis* (14.8%), *C.* aff. *viridis* sp. A (6.6%) and *Cl.* cf. *aurivillii* (5.1%). Species-specific dbRDA bubble plots (Fig. 7) indicate that this is driven primarily by higher recruitment of *C. orientalis* at locations where adult populations were already more established. Recruitment of *C.* aff. *viridis* sp.

**Table 3. Results of permutational multivariate analysis of variance (PERMANOVA) of the significance of differences in the composition of the local substrate, recruitment block benthos and local adult bioeroding community**

SS, sum of squares; MS, mean square

| Factor | d.f. | SS | MS | Pseudo *F* | $P_{perm}$ |
|---|---|---|---|---|---|
| Local substrate | | | | | |
| Site | 6 | 255.09 | 42.514 | 5.6117 | 0.001 |
| Depth | 1 | 29.118 | 29.118 | 3.8435 | 0.001 |
| Site × depth | 6 | 89.538 | 14.923 | 1.9698 | 0.001 |
| Residual | 51 | 386.38 | 7.576 | | |
| Total | 64 | 768 | | | |
| Recruitment block benthos | | | | | |
| Site | 1 | 8.4527 | 8.4527 | 0.91856 | 0.529 |
| Depth | 6 | 97.837 | 16.306 | 1.772 | 0.002 |
| Site × depth | 6 | 66.141 | 11.023 | 1.1979 | 0.172 |
| Residual | 51 | 469.31 | 9.2021 | | |
| Total | 64 | 640 | | | |
| Local adult bioeroding sponges | | | | | |
| Site | 1 | 1185.4 | 1185.4 | 2.2846 | 0.047 |
| Depth | 6 | 10289 | 1714.9 | 3.3053 | 0.001 |
| Site × depth | 6 | 4500 | 750 | 1.4455 | 0.072 |
| Residual | 51 | 26461 | 518.84 | | |
| Total | 64 | 42602 | | | |

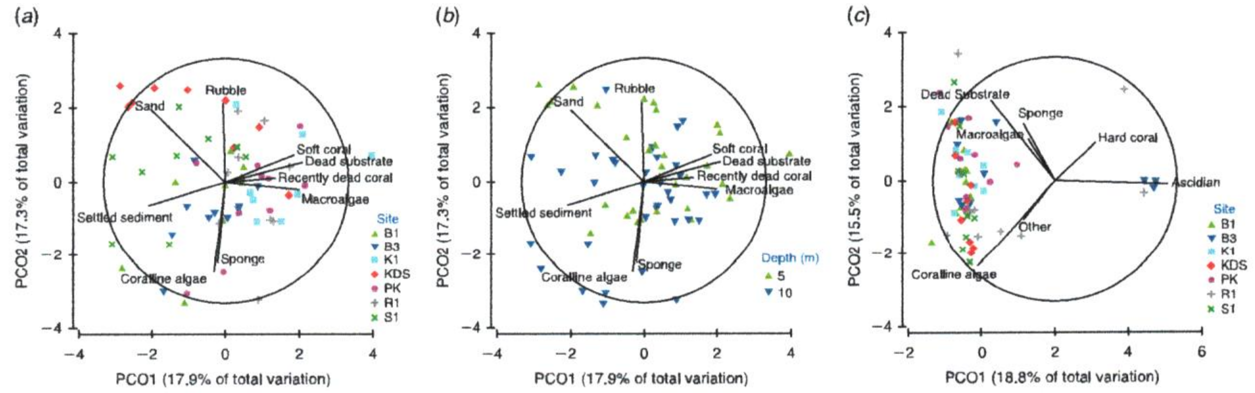

**Fig. 4.** Two-dimensional representation (principal coordinate analysis; PCO) of benthic community composition of the substrate adjacent to (*a*, *b*) and on the recruitment blocks (*c*). (*a*, *b*) The same PCO is shown, but points are either designated by site (*a*) or depth (*b*). Overlaid vectors represent substrate components that have a Pearson's correlation coefficient >0.4 with either of the PCO axes. B1, Buoy 1; B3, Buoy 3; K1, Kaledupa 1; KDS, Kaledupa Double Spur; PK, Pak Kasim's; R1, Ridge 1; S1, Sampela 1.

B was also associated with locations where the adult population of *Cl.* cf. *aurivillii* was high. Variation in flow and substrate composition (both adjacent to and on the recruitment blocks) explained 31.3% of variation in the recruit assemblage (Table 4); the best DistLM model selected flow (14.5%), macroalgae (3.6%) and bare substrate (3.2%) on the recruitment blocks, and algae-covered dead coral (4.3%), recently dead coral (2.9%) and rubble (2.8%) adjacent to the recruitment blocks. Species-specific dbRDA (Fig. 8) bubble plots indicate that recruitment of both *Cl.* cf. *aurivillii* and *C.* aff. *viridis* sp. B was associated with low-flow sites and a higher cover of recently dead cover in adjacent benthos. The recruitment of *C. orientalis* was more associated with higher-flow sites with low rubble and macroalgae cover in the adjacent benthos.

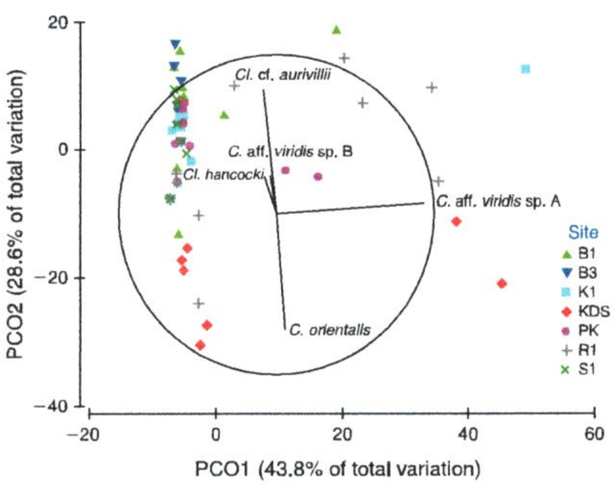

**Fig. 5.** Two-dimensional representation (principal coordinate analysis; PCO) of recruitment block similarities with regard to their adjacent bioeroding sponge assemblage composition. Overlaid vectors represent Pearson's correlation of the same data with either of the PCO axes. Only *Cliothosa* (*Cl.*) cf. *aurivillii*; *Cliona* (*C.*) *orientalis* and *C.* aff. *viridis* sp. A have correlation coefficients >0.4. B1, Buoy 1; B3, Buoy 3; K1, Kaledupa 1; KDS, Kaledupa Double Spur; PK, Pak Kasim's; R1, Ridge 1; S1, Sampela 1.

## Discussion

Over the course of this 2-year study, five species of bioeroding sponge were observed to have recruited to most of the deployed experimental blocks, across all sites and depths. Species composition of recruit assemblages was distinctly different among sites, apparently due to species-specific differences in the effects of philopatry, hydrodynamic regime and substrate cues. Although spatial cover of the recruits was generally low compared with the adult cover of these sponges in the region (Marlow *et al.* 2018*a*), compared with other studies (Kiene and Hutchings 1994; Pari *et al.* 1998, 2002) the proportion of blocks that exhibited bioeroding sponge recruitment was very high for this length of study.

Total bioeroding sponge recruitment and assemblage composition was associated with the local abundance of adult bioeroding sponges, suggesting limited larval dispersal (or a preference for larval settlement among conspecifics) for some species. Although it is impossible to be conclusive about dispersal without the use of genetic markers, *ex situ* larval manipulation or *in situ* larval sampling (e.g. Mariani *et al.* 2006; Whalan *et al.* 2008; Chaves-Fonnegra *et al.* 2015), the results of this study suggest limited larval dispersal for *C. orientalis* and a wider dispersal for *C.* aff. *viridis* sp. B and *Cl.* cf. *aurivillii*. Recruitment of *C. orientalis* at sites where this species was already well established is consistent with the limited larval dispersion of the Mediterranean bioeroding sponge *C. viridis*, which is highly correlated with the abundance of adults (Mariani *et al.* 2000). The correlation is attributed to clusters of eggs adhering to the substratum adjacent to 'mother' sponges and the predominantly crawling behaviour of larvae (Mariani *et al.* 2000, 2001, 2006). Heightened larval settlement in the presence of conspecific larvae (and to a lesser extent adults) is also known to occur in sponges (Ettinger-Epstein *et al.* 2008). Limited dispersal and philopatric aggregated recruitment is thought to facilitate settlement to favourable habitats (Pawlik 1992), and is particularly important for zooxanthellate bioeroding sponges (such as *C. orientalis* and *C. viridis*) that require a well-lit calcareous habitat (López-Victoria and Zea 2005). The alternative strategy of a wider dispersal by *C.* aff. *viridis* sp. B

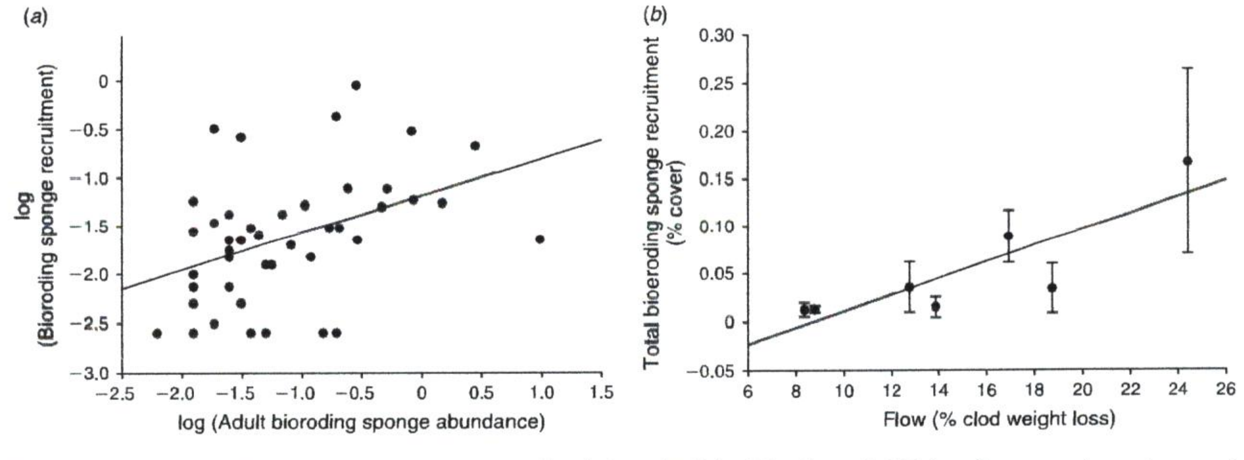

**Fig. 6.** Total bioeroding sponge recruitment (percentage cover) in relation to the (*a*) local abundance of adult bioeroding sponges (percentage cover) and (*b*) average water flow. Note data in (*a*) are represented on log axes; error bars in (*b*) represent the s.e.m.

**Table 4. Table of sequential test results of biotic and abiotic predictor variables selected as the best solution for bioeroding sponge recruitment by distance-based linear model (DistLM) analyses**

AICc, Akaike's information criterion corrected for small sample size; SS, sum of squares; proportion of variation; cumulative proportion of variation

| | AICc | SS (trace) | Pseudo-*F* | *P* | Prop. | Cumul. |
|---|---|---|---|---|---|---|
| Species (adult bioeroding sponges) | | | | | | |
| *Cliona orientalis* | 422.3 | 7036.3 | 10.976 | 0 | 0.1484 | 0.1484 |
| *Cliona* aff. *viridis* sp. A | 419.2 | 3121.2 | 5.1926 | 0.01 | 0.0658 | 0.2142 |
| *Cliothosa* cf. *aurivillii* | 417.1 | 2438.9 | 4.2717 | 0.01 | 0.0514 | 0.2656 |
| Factor (local substrate, block benthos and flow) | | | | | | |
| Flow | 422.5 | 6871.6 | 10.675 | 0 | 0.1449 | 0.1449 |
| Algae-covered dead coral (adjacent substrate) | 421.3 | 2060 | 3.3181 | 0.02 | 0.0434 | 0.1883 |
| Macroalgae (block) | 420.7 | 1697.9 | 2.8148 | 0.04 | 0.0358 | 0.2241 |
| Bare substrate (block) | 420.3 | 1499.3 | 2.5488 | 0.05 | 0.0316 | 0.2558 |
| Recently dead coral (adjacent substrate) | 420.2 | 1376.5 | 2.3943 | 0.09 | 0.029 | 0.2848 |
| Rubble (adjacent substrate) | 420.1 | 1345.1 | 2.3951 | 0.04 | 0.0284 | 0.3131 |

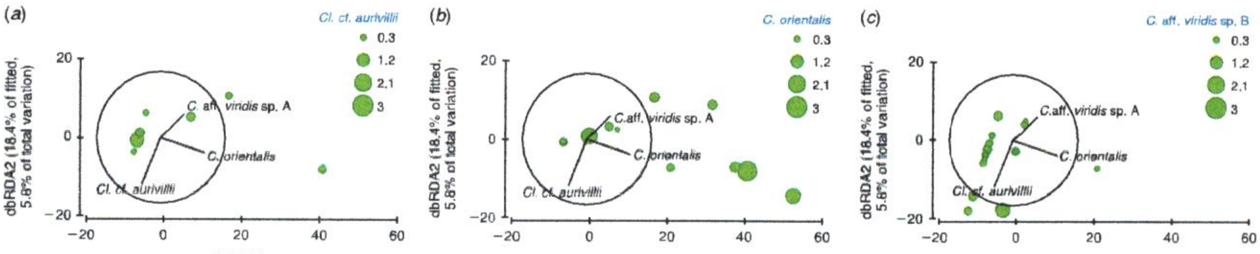

**Fig. 7.** Distance based redundancy analysis (dbRDA) ordinations of fitted models for recruit assemblage composition in relation to adult population. Overlaid two-dimensional bubbles represent recruit abundance of (*a*) *Cliothosa* cf. *aurivillii*, (*b*) *Cliona orientalis* and (*c*) *Cliona* aff. *viridis* sp. B. Overlaid vectors represent adult abundance components that were selected by the distance-based linear model (DistLM) analysis.

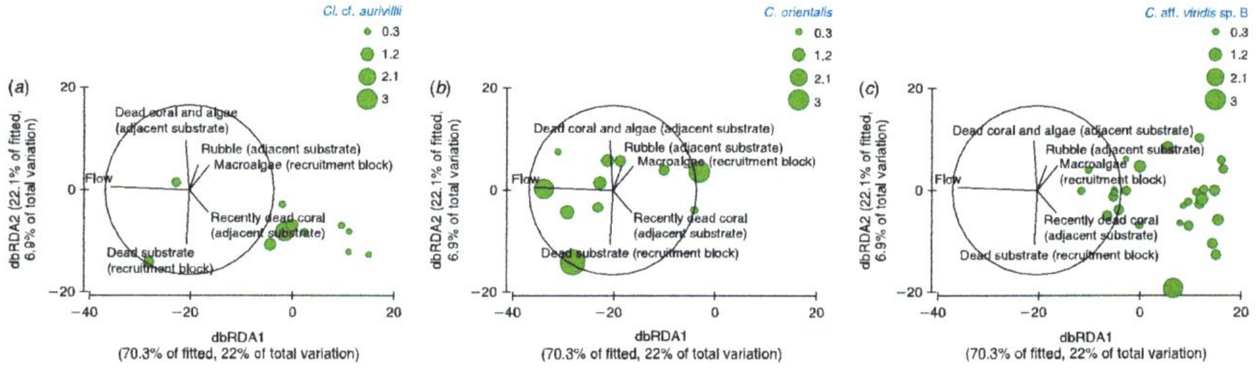

**Fig. 8.** Distance based redundancy analysis (dbRDA) ordinations of fitted models for recruit assemblage composition in relation to flow and substrate composition (both adjacent to and on the recruitment blocks). Overlaid two-dimensional bubbles represent the recruit abundance of (*a*) *Cliothosa* cf. *aurivillii*, (*b*) *Cliona orientalis* and (*c*) *Cliona* aff. *viridis* sp. B. Overlaid vectors represent components that were selected by the distance-based linear model (DistLM) analysis.

and *Cl.* cf. *aurivillii* is likely to incur greater presettlement mortality, but also has a greater chance of avoiding localised extinction (Uriz *et al.* 1998; Maldonado 2006).

Dispersal distance is likely to be a consequence of not just larval mobility, but also local hydrodynamics, which was found to affect recruit abundance and assemblage composition. Overall recruitment was greatest at the two sites with the highest degree of water movement (KDS and R1) and least at the sites with lowest water movement (B1 and B3). Research on the tropical non-bioeroding sponge *Carteriospongia* *foliascens* (Abdul Wahab *et al.* 2014) has shown that hydrodynamics can have a positive effect on fecundity, with consequentially higher recruitment. This may explain the generally lower recruitment levels on reefs with a low degree of water movement where *C.* aff. *viridis* sp. B was the only species to recruit in considerable numbers. Interestingly, the high overall recruitment at the high-flow sites was largely influenced by the recruitment of *C. orientalis* on these reefs. It may be assumed that a high degree of water flow would increase larval dispersal and not the philopatry observed in this species. However, increased flow may also promote fecundity in the local adult sponge population, as has been shown in *C. foliascens* (Abdul Wahab *et al.* 2014). Furthermore, crawling larvae may be decoupled from the effects of high flow rates at the reef level because they are able to manoeuvre within the boundary layer, where they are subject to much less flow speed and turbulence than midwater larvae (Maldonado 2006).

Evidence for the effects of substrate cues on recruitment was not as consistent as that of flow or localised adult population, but there were some associations that warrant discussion. The most consistent was the presence of algae-covered dead coral in substrate adjacent to the recruitment blocks, which was negatively correlated with overall recruitment and was the strongest substrate indicator in the DistLM analysis. Algae, particularly macroalgae, have consistently been shown to be a strong spatial competitor with bioeroding sponges (López-Victoria *et al.* 2006; Chaves-Fonnegra and Zea 2011; González-Rivero *et al.* 2012, 2016) and are known to deter the settlement of invertebrate larvae, such as corals (Arnold *et al.* 2010). Moreover, a recent assessment of bioeroding sponge cover on the GBR (Ramsby *et al.* 2017) found that increases in the abundance of *C. orientalis* were most likely to occur on reefs with low macroalgal cover. The results of the present study suggest that this could be due to enhanced recruitment at these sites. To a lesser degree, the DistLM analysis also showed that recruitment (particularly *Cl.* cf. *aurivillii* and *C.* aff. *viridis* sp. B) was associated with higher cover of recently dead coral and coral rubble in the adjacent substrate. This positive relationship strengthens the suggestion that recruitment on uncolonised calcareous substrate is favoured among presettlement bioeroding sponge larvae (López-Victoria and Zea 2005), potentially due to unique microbial biofilms, which are increasingly recognised as important for initiating settlement in sponges and other marine invertebrates (Whalan *et al.* 2008; Abdul Wahab *et al.* 2011; Whalan and Webster 2014).

Three locally extant species, namely *C.* cf. *schmidtii*, *S.* cf. *vagabunda* and *Z. criceta*, did not recruit to the experimental substrates during the 2-year deployment. Interspecies differences in recruitment rates could be due to interspecies differences in fecundity or due to number of pre- and post-settlement factors. Although many bioeroding sponge species have single annual reproductive events (Mariani *et al.* 2000; Rosell and Uriz 2002; Piscitelli *et al.* 2011; González-Rivero *et al.* 2013), recruitment in some species of sponges can often vary interannually, with 'pulses' of high recruitment occurring in some years and not in others (e.g. McMurray *et al.* 2010). For these 'pulse' species (e.g. *S. vagabunda*; Kelly 1986), the time scale of this study may have been insufficient to detect recruitment. The sides of the recruitment blocks were also all equally exposed, which could possibly deter settlement by sponges with a preference for cryptic habitats. Numerous studies have found large differences in sponge abundance between cryptic and exposed surfaces (Maldonado and Young 1996; Stubler *et al.* 2016), which is thought to be a function of negative phototaxis in settlement, reduced exposure to predators or settled sediment (Maldonado and Young 1996). Species such as *C.* cf. *schmidtii* that are more common in cryptic habitats (J. Marlow, pers. obs.) may require more cryptic substrate for recruitment than offered by the recruitment blocks.

The recruitment of bioeroding sponges to the majority of experimental substrates after only 2 years of deployment in the Wakatobi is considerably more rapid than in other comparable studies. A deployment of experimental substrates by Tribollet *et al.* (2002) in the GBR found no bioeroding sponge presence after 12 months of deployment. A similar absence of bioeroding sponges was found after 15 months of deployment on Palmyra Atoll in the central Pacific (Elmer 2016) and after 24 months in French Polynesia, where only 5% of experimental substrates were colonised by bioeroding sponges (Pari *et al.* 1998). Kiene and Hutchings (1994) found a similar trend around Lizard Island in the GBR, and suggested that succession to bioeroding sponge occupation may take ≥4 years to appear after substrate becomes available. The disparity between the studies could be due to differences in the timing and investment of reproductive output between the respective species assemblages or differences in adult population densities (Kelly 1986; McMurray *et al.* 2010).

Our observations of rapid bioeroding sponge recruitment indicate that coral mortality in the region could benefit these sponges. Successful species are likely to have reproductive modes that allocate considerable amounts of energy to egg production (e.g. *C. viridis*; Mariani *et al.* 2001; Piscitelli *et al.* 2011), have multiple intra-annual spawning events (e.g. *C. delitrix*; Chaves-Fonnegra *et al.* 2016) or exhibit constant recruitment (e.g. *C. tenuis*; González-Rivero *et al.* 2013) or chance-related recruitment in the cases of those that recruit at more irregular intervals (e.g. *S. vagabunda*; Kelly 1986). In addition, although wider larval dispersal (e.g. *Cl.* cf. *aurivillii* and *C.* aff. *viridis* sp. B) is generally considered more opportunistic (Mariani *et al.* 2006), species that have more restricted dispersal (e.g. *C. orientalis*) are potentially able to proliferate on more local scales (Uriz *et al.* 1998).

In conclusion, coral mortality may increase the availability of calcareous habitat for bioeroding sponges but recruitment to these novel substrates could also be reliant upon the proximity of adult populations and local hydrodynamics. Although species with wider larval dispersal may benefit from more regional scales of coral mortality (given the right settlement cues), more limited dispersal strategies could result in localised proliferation and even dominance on some degraded reefs.

## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Declaration of funding

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